

Comparative Population Biology of Critically Endangered *Dracocephalum austriacum* (Lamiaceae) in Two Distant Regions

Tomáš Dostálek · Zuzana Münzbergová

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Abstract Our study aims to compare the population dynamics of critically endangered species, *Dracocephalum austriacum*, in two distant regions (Czech and Slovak Karst) with similar habitat conditions, and to evaluate if conclusions concerning factors affecting population performance in one region could help in understanding species dynamics in the other region. Transition matrix models were used to examine population dynamics of the species. Results show that populations in the Slovak Karst are performing better than populations in the Czech Karst. The transitions contributing most to the population growth rates were those of stasis in the small and large adult plant stage. These transitions are, however, stable between populations and years, suggesting that they are not very sensitive to the ongoing changes. Transitions that contribute most to variations in population growth rate include seed and seedling production by large adult plants, seed germination and stasis and growth of small adult plants. These transitions seem to be affected by habitat conditions (soil depth and bare rock cover), genetic parameters of the populations, climate fluctuations (especially severe droughts), and shrub expansion. The transitions contributing most to the population growth rates are very similar between the regions except for contributions of seedling growth and stasis of large adults. These differences need to be considered before using information about the most important life cycle transitions in other regions. We suggest that similar results would be found for other species with narrow habitat requirements occupying very similar habitats, even in very distant regions.

Electronic supplementary material The online version of this article (doi:10.1007/s12224-012-9132-2) contains supplementary material, which is available to authorized users.

T. Dostálek (✉) · Z. Münzbergová

Institute of Botany, Academy of Sciences of the Czech Republic, Zámek 1, CZ-252 43, Průhonice, Czech Republic

e-mail: tomas.dostalek@gmail.com

T. Dostálek · Z. Münzbergová

Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Prague 2, Czech Republic

Keywords Elasticity · Environmental variations · Europe · Genetic diversity · Life table response experiments · Population dynamics · Rare species

Introduction

In spite of the general interest in understanding spatial and temporal variations in population dynamics (e.g., Oostermeijer et al. 1996; Fréville et al. 2004; Ehrlén et al. 2005; García 2008), most knowledge concerning spatial variation comes from studies focusing only on a single small region. Only four studies that have analyzed population dynamics at more than one site in different regions are known (Menges and Dolan 1998; Hyatt and Araki 2006; Eckstein et al. 2009; Jongejans et al. 2010). For example, Jongejans et al. (2010) compared the population dynamics of three Asteraceae species over a range of European populations, and demonstrated large variations in the life-histories of the plants, as well as strong interactions between years and areas. This indicates that factors affecting population dynamics of the species largely differ between regions and that fluctuations in population dynamics due to climatic conditions are not synchronized across distant regions.

Understanding variations in population dynamics over large spatial scales may be important for models of species dynamics over its entire range, e.g., in the framework of climate change (Thuiller et al. 2008). Important tools in such studies are matrix transition models, which are commonly used to describe the life cycle of a species. When applied to rare and endangered or invasive species, transition matrix models may be used to design optimal management actions for protecting or eradicating the species in a given area (e.g., Crouse et al. 1987; Menges 1990; Martínez-Palacios et al. 1999; Parker 2000; Koop and Horvitz 2005; Thomson 2005; Pino et al. 2007). Wider application of the models is hindered because collecting detailed demographic data is very laborious and time demanding. It is therefore appealing to use knowledge on population dynamics and resulting conclusions on optimal management obtained from one region (and/or species) in other regions (and/or closely related species).

As suggested above, such a transfer of knowledge may not be easy, because different populations may be adapted to different environmental conditions, and thus may respond differently to given variations in local conditions. A large source of this variation in population dynamics between different populations are often the significant differences in local habitat conditions (e.g., Oostermeijer et al. 1996; Ehrlén et al. 2005). Such differences can even manifest between populations that are very close in space, if they are growing in very different local conditions. Thus, we assume that use of knowledge of one population to design management of another population will be mainly possible if populations occur in similar habitat conditions.

In the present study, the population dynamics of a critically endangered plant species, *Dracocephalum austriacum* L. (Lamiaceae, Fig. 1) is compared in two distant regions. In both regions, the populations occur in comparable habitats of rocky steppes and rocky sunny slopes. The species thus has very narrow habitat requirements. Compared to previous studies comparing plants from distant regions (Menges and Dolan 1998; Hyatt and Araki 2006; Eckstein et al. 2009; Jongejans et al. 2010) our comparison deals with localities that are geographically far away, but have



Fig. 1 Photos of the *Dracocephalum austriacum* population (left) and an individual plant (right). Photos were taken at the locality, Kodsská stěna (C4) in the Czech Karst region

very similar habitat conditions. It can be predicted that transfer of knowledge between the two regions should be easier than in previous examples.

D. austriacum is endangered over its entire distribution range, and is of interest for nature conservation efforts in a wide range of countries (Fig. 2). Recently, this species has been identified in only nine localities in the Czech Republic, some with only a few individuals at risk of local extinction (Čeřovský 1999; Dostálek et al. 2010). A very similar situation exists in the neighboring Slovak Republic (Čeřovský 1999;

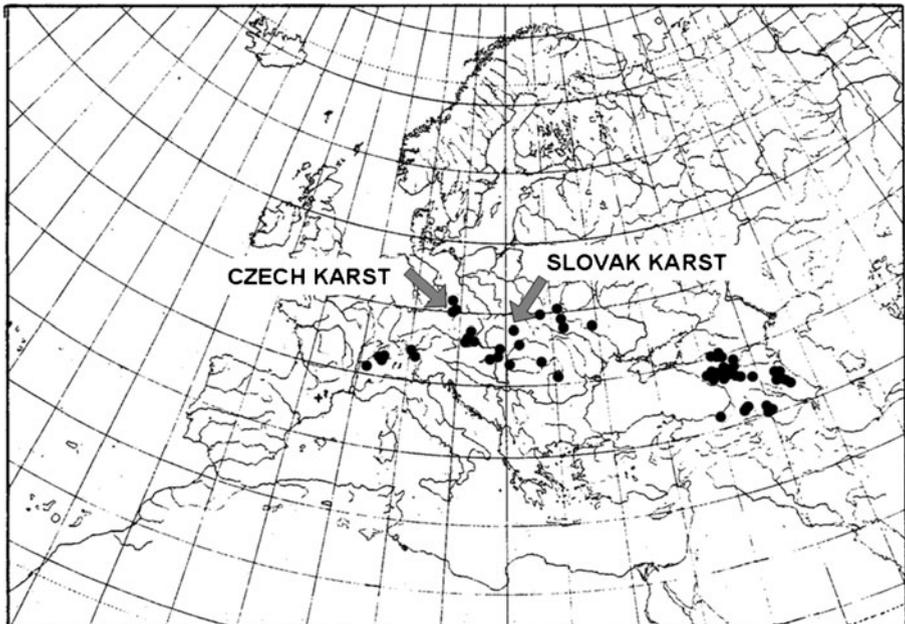


Fig. 2 Distribution range of *Dracocephalum austriacum*. Dots show separate localities. Arrows indicate studied regions of the Czech and Slovak Karst. This figure was modified from Meusel et al. (1978)

Dostálek et al. 2010), and in other countries (Council of European Communities 1992). Detailed population dynamics of the species in two distant regions were studied in the attempt to answer the following questions: *i*) What is the spatial and temporal variability in the population dynamics of this species? *ii*) What are the differences in population dynamics between populations in two distant regions of the Czech and Slovak Karst? *iii*) Can something be learned about population dynamics in one region from knowledge of population dynamics in another region?

Methods

Study Species

Dracocephalum austriacum L. (Lamiaceae) is a perennial herb or dwarf shrub, with erect or ascending stems up to 60 cm high, which grows on rocky steppes and rocky sunny slopes (Hrouda 2002) (Fig. 1). The species is diploid ($2n=14$) (Heywood 1980), and flowers from the second half of May through the first half of June. According to our data, single individuals of *D. austriacum* can survive for several decades (Dostálek 2009). The species does not reproduce clonally.

D. austriacum is listed as a critically endangered species in the Czech and Slovak Republics (Holub and Procházka 2000), and is a species of high conservation interest in Europe (Council of European Communities 1992). Localities of *D. austriacum* are very often overgrown with shrubs and trees and thus shrub and tree encroachment reduction programs are the prevailing management approach in both regions. The distribution range of this species is discontinuous, and ranges from the eastern Pyrenees, across France, Italy, Switzerland, Austria, the Czech Republic (which constituted the northern edge of the distribution range), the Slovak Republic, Hungary, Romania, Ukraine, and the Caucasus (Meusel et al. 1978) (Fig. 2).

Localities

For more information about the current and past distribution ranges of *D. austriacum* in the Czech and Slovak Republics, see Dostálek et al. (2010). To study demographic parameters, we selected three populations from the Landscape Protected Area of the Czech Karst (Císařská rokle – C1, Haknovec – C2 and Kodská stěna – C4) and the three largest populations in National Park Slovak Karst (Zádielský kameň – S1, Domické škrapy – S2 and Železná vrata – S3). The codes of these localities were chosen to be consistent with our previous study (Dostálek et al. 2010). The selected populations had at least 100 plants to obtain good estimates of demographic parameters. The Czech localities are within 5 km of each other and the Slovak localities are within 33 km of each other. The distance between the two regions is approximately 500 km (Fig. 2). The Czech and Slovak localities used in this study have similar habitat conditions. In both regions, plants are growing on limestone slopes together with shrubs and grasses. Still, there are significant differences in species composition on *D. austriacum* localities between the two Karst regions. The species prevailing in the Slovak Karst localities include, e.g., *Thesium linophyllum* and *Vincetoxicum*

hirundinaria. The species prevailing in the Czech Karst include, e.g., *Galium glaucum*, *Sedum sexangulare* and *Stipa pennata* (Dostálek 2005).

Data Collection

We tagged 100–200 individuals in each population (usually all plants in the locality, with the exception of a few individuals on poorly accessible steep slopes), and recorded the number of vegetative and flowering stems per plant in June or July at the time of fruiting, for a period of 4 years (2003–2006). The number of stems was used for classification of the plants into life-cycle stages (see below).

Each year (2003–2005), at the beginning of the transition interval, seed production was estimated at each studied locality in 20 randomly selected flowering plants, by counting the number of black or dark-brown hard seeds. After counting, seeds were left at the localities. Furthermore, each year at each locality samples of 100 black or dark-brown hard seeds were taken, cut and visually checked to see if the embryo was developed (in some cases, the embryo is aborted even though the seed looks well developed from outside). Seed production was then estimated as number of seeds produced per plant times the proportion of viable seeds recognized by cutting.

D. austriacum seeds have a hard coat and are expected to survive in soil for many years. To estimate a species' ability to survive in the seed bank, 10 nylon bags, each containing 50 seeds, were buried at two places in C2 locality in October 2010. Two bags from each place were excavated in October 2011 and the seeds were tested for viability. The tip of each seed was cut so that water could come inside easily. The seeds were regularly watered with distilled water on Petri dishes and kept in a growth chamber under a fluctuating regime (12 h light at 20 °C, 12 h dark at 5 °C). Germinated seeds were regularly removed. The dishes were kept until all the seeds germinated or decayed (approximately 2 months). The same procedure was used to estimate the viability of fresh seeds to provide a baseline from which to estimate the decline in germination over time (Münzbergová 2005). Comparison of the germination approach to estimating seed viability with detection of viability of embryo by cutting the seed (as described above) indicated that these two approaches provide largely comparable results. This experiment was conducted only at the C2 locality (the largest one) because of problems in getting enough seeds for the experiment. Therefore, we assumed the seed bank stasis (a_{11}) to be constant throughout all localities. There were 97 viable seeds out of 200 fresh seeds entering the seed bank. After one year in the soil, we recorded 56 viable seeds out of 200 buried seeds. Therefore, the seed bank stasis (a_{11}) was calculated as: $a_{11}=56/97=0.577$.

To estimate germination from the seed bank (transition a_{21}), the number of seeds in the seed bank in each locality (SD_{all}) was estimated. To calculate the number of seeds in the seed bank on locality i (SD_{all-i}), we used data on mean seed production per locality i in 2003–2006 (SD_{0306i}) and the seed bank stasis (a_{11}):

$$SD_{all-i} = \sum_{n=0}^{\infty} SD_{0306i}(a_{11}^n),$$

where n is number of years in the seed bank from 0 to infinity (in practice for 50 years). In this way, the number of seeds that accumulated in the locality's seed bank over the course of existence of the population was calculated.

The seed bank stasis was only estimated from 2 years experiment and we thus could not directly assess between year variability and long term seed bank stasis. That is why we also calculated population growth rates using decreased seed stasis probabilities (by 10 % and 20 %) and explored how this variable influenced population growth rates. This analysis showed that a decrease in seed stasis of 10 % and 20 % results in a 0.1 %–0.2 % and 0.2 %–0.4 % decrease in the population growth rate. This indicates that the seed bank stasis has relatively little effect on the performance of the populations. A model with seed bank incorporated in the life cycle (as described above) was compared with a model without seed bank (i.e., relating number of new seedling directly to the number of small and large adult individuals) and the results were quite similar. Thus we decided to use a model with the seed bank to better describe the population dynamics of the studied species.

To estimate seed germination, the number of new seedlings each year was counted at each locality (in most localities all seedlings in the entire locality were counted – see Table 1 for locality size).

Matrix Model Construction

Plants were classified into four stages: seeds, seedlings, small adult plants and large adult plants (Fig. 3). Seedlings were defined as plants with only one thin vegetative stem up to 10 cm high. These were plants that germinated in the year they were recorded or 1 year before. There was no seedling older than 2 years (in 2 years the seedling develops into an adult plant that can flower). Because of the few seedlings in some years and localities (see Tables S1, S2 in Electronic Supplementary Material, hereafter ESM), only one seedling stage was maintained instead of two (1-year-old seedlings and 2-year-old seedlings), which enables more than 2-years stasis in the seedling stage in the model. However, both approaches were compared and no substantial differences in the results were found. Therefore, we decided to keep the simple model with one seedling stage. Small adult plants were defined as plants with one stem higher than 10 cm, or with 2–5 stems. Large adult plants were defined as plants with six and more stems. The specific division of adult plants into small and large plants was motivated by an attempt to have groups of plants with similar behavior, and a sufficient number of individuals in each category. A significantly higher probability of survival and flowering in plants with more than five stems was found, and thus this value was used to delimit the boundary between small and large adult plants. Identification of a sufficient number of individuals in each category is an important condition for obtaining reliable estimates of transition probabilities (Münzbergová and Ehrlén 2005). In bad years or during senescence, plants can shrink, and thus move from the large adult plant stage to the small adult plant stage. This transition is referred to as retrogression (a_{34}). Seed dispersal was not considered in the model. The seeds are heavy with no adaptation to dispersal and thus likely disperse to very short distances and thus most seeds stay within populations. In large populations, the sampling plots were placed within relatively homogenous stands of *D. austriacum* and thus the number of seeds leaving the sampling plots was

Table 1 List of *Dracocephalum austriacum* populations and population characteristics

Population	Altitude (m a.s.l.)	Slope (m)	Orientation	Pop area (m ²)	Soil depth (cm)	Shrubs (%)	Bare rock (%)	H_E	H_O	F_{ST}	F_{IS}	Pop size	λ_S
Czech Karst													
C1 – Cisařská rokle	270	30°–80°	E	75	4.33	15	50	0.055	0.046	0.213	0.168	211	1.032
C2 – Haknovec	287	40–60°	S, SW	150	4.54	5	40	0.128	0.114	0.151	0.103	640	1.083
C4 – Kodská stěna	350	35–90°	S	140	5.73	2	30	0.132	0.082	0.177	0.378	181	1.017
Slovak Karst													
S1 – Zádielský kameň	595	30°	SW	75	4.88	20	25	0.183	0.112	0.183	0.385	100	1.153
S2 – Domické škrapy	340	3°	SW	200	13.72	5	5	0.171	0.114	0.187	0.336	200	1.060
S3 – Železné vráta	730	5–10°	S, SW	100	9.19	7	15	0.167	0.141	0.165	0.154	150	1.066

H_E – expected heterozygosity, H_O – observed heterozygosity, F_{ST} – mean genetic distance to other populations, F_{IS} – inbreeding coefficient, Pop size – population size, Pop size – population size in 2005, λ_S – stochastic population growth rate 2003–2006.

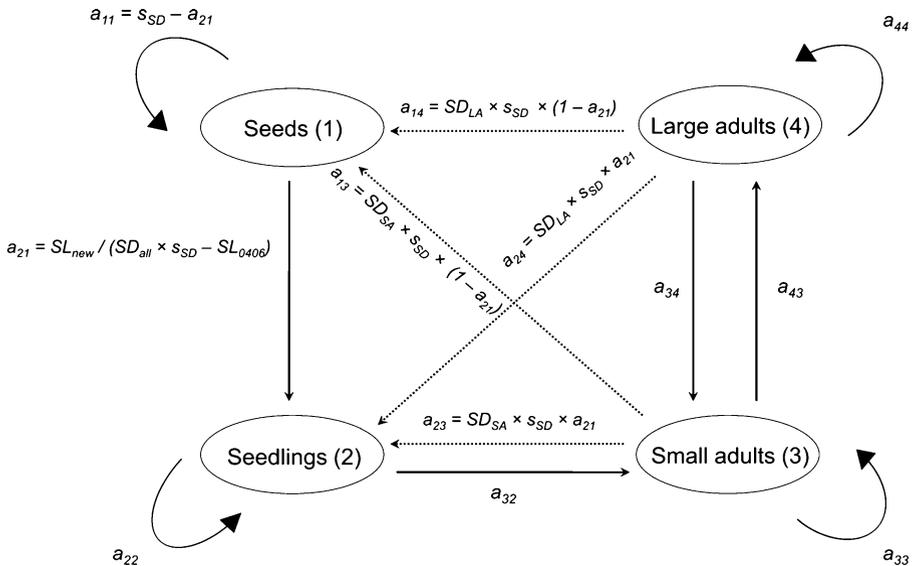


Fig. 3 Life-cycle graph of *Dracocephalum austriacum*, representing reproduction (dotted lines) and transitions of individuals between stages (solid lines). The matrix elements (a_{ij}) are probabilities of transitions between stages. s_{SD} – seed bank stasis, SL_{new} – number of new seedlings on locality, SL_{0406} – mean number of new seedlings established on locality in 2004–2006, SD_{all} – number of all viable seeds present on locality, SD_{SA} – mean number of seeds produced by small adult plant (stage 3), SD_{LA} – mean number of seeds produced by large adult plant (stage 4)

approximately equal to that arriving by dispersal (Münzbergová 2007). In smaller populations all individuals from the population were included in the study and seedlings were also searched for in the area 3 m from the edge of the populations to check for seedlings dispersing outside the population (no such seedling was however detected) – Fig. 3. We did not explicitly include density dependence in our model because we do not have any data about density dependence. Moreover it is hardly possible to perform manipulative experiments and study density dependence effect with such a critically endangered species. We do not suppose that density effects play an important role in *D. austriacum* populations because there are usually quite a lot of free gaps for establishment of new plants in the habitat. Actual intra- and interspecific density effects are, however, implicitly included in the parameter values.

Comparison of Life-History Traits

Differences in the probability of mortality, flowering, retrogression and growth between the two distant regions were tested using logistic regression in S-Plus (MathSoft, Inc. 2000) (cf. Münzbergová 2007). Because these parameters were determined in individuals of different sizes, the stage in the previous year was used as another independent variable in these tests. In addition, data were collected for the three transition intervals and from different populations, and thus year and population (nested within region) were incorporated as other independent variables. The effects of interactions between region and all other independent variables were tested as well. Differences in the number of seeds produced per flowering stem between the two

regions were also tested using GLM with Gamma distribution in S-Plus (MathSoft, Inc. 2000). Region, year, population nested within region, and their interactions were used as independent variables. In these analyses, all factors were fixed.

Population Performance

Demographic data were examined using transition matrix models (Caswell 2001). In this study, the finite rate of increase (λ , population growth rate) was calculated for each population and transition interval. Elasticity was also calculated, although it is usually used as a measure of the contribution of a matrix element to fitness (de Kroon et al. 2000).

To summarize information on population growth rates over region, population and years, we used a stochastic simulation approach as suggested by Caswell (2001) and Bucharová et al. (2010). A sequence of matrices was drawn for each set of matrices; each matrix from the set was drawn at random and with equal probability, and population growth was simulated using this matrix sequence. Each simulation was conducted for 10^5 , one-year intervals. This stochastic population growth rate is referred to as λ_S . Using this approach we incorporate environmental stochasticity within region, population and year into the model and into estimates of λ and elasticity values. Simulations were performed using a MATLAB script developed in a previous study (Münzbergová 2005).

Each estimate of transition probability, and thus each estimate of population growth rate and elasticity, is confined by an error, because of the limited number of individuals that can be sampled. To estimate this error, bootstrap confidence intervals of the population growth rates were calculated (Alvarez-Buylla and Slatkin 1994). This was done by bootstrapping original data used to derive the original matrices 1,000 times. Based on these results, confidence intervals for the population growth rates were constructed for each population and region (Efron and Tibshirani 1993). The above-described bootstrap approach estimates the effects of demographic stochasticity because it estimates population growth rate in situations when randomly some individuals with a given fate are missing from the population and some others are there multiple times. Therefore confidence intervals take into account the possible effects of demographic stochasticity in our data. A MATLAB script developed for this purpose in previous studies was used (Münzbergová 2006, 2007). To estimate confidence intervals for the overall growth rate and elasticity of one factor (year, population, region), the bootstrapped matrices were also combined using stochastic simulation as described above. These confidence intervals enable estimation of the variation in single parameters, but do not provide estimates of the significance of difference between transition matrices or their combinations (Caswell 2001). To estimate this, a permutation test was performed, permuting single individuals used to estimate transition probabilities between each pair of populations or between each pair of types of populations (combined matrices of a given type; e.g., year, population and region). In each permutation run, differences in population growth rates between the pair of populations or pair of types of populations were estimated, and the number of permutation runs in which the absolute value of the difference was larger than the observed difference was counted. This value was then used to estimate the probability that observed differences between each pair of populations or pair of types of

populations could be random. For these purposes, a MATLAB script developed by Münzbergová (2007) was used.

A life-table response experiment (LTRE) with fixed factorial design was conducted to examine the effect of population within a region, the effect of single life stage transitions within a region, and the effect of year within regions on population growth rate (Caswell 2001). For details of the methods used, see Münzbergová (2007). LTRE analysis assesses the contribution of each life cycle transition to differences between different levels of each factor (i.e., population within a region, single life-stage transitions within a region, year within regions). Important life-cycle transitions are those with large positive contributions to some factor levels and large negative contributions to others. Analogously to ANOVA, the mean of the treatment is zero. The significance of LTRE analysis was evaluated by performing a permutation test, in which individuals were permuted between the categories under comparison (i.e., population within a region, single life-stage transitions within a region, year within regions) and the LTRE was repeated using these permuted data. We then calculated how often the overall contribution and the contribution of each matrix element were bigger than would be expected if the individuals were randomly distributed among the groups. This value was used as a significance value, to identify the matrix elements that significantly contribute to differences between categories being compared. A MATLAB script was used to perform the analysis and 10^5 permutations were used in each case.

All analyses were performed using Matlab, version 7.3.0.267 (The MathWorks, Inc., Natick, Massachusetts, USA).

Data on Habitat Conditions in the Populations

To understand variations in population performance, soil depth was recorded, measured in the vicinity of 20 randomly chosen flowering plants (see Data Collection above). Information on the following genetic parameters obtained during our previous allozyme study (Dostálek et al. 2010) was also incorporated: H_E (mean expected population heterozygosity), H_O (mean observed population heterozygosity), F_{ST} (mean genetic distance from other populations), F_{IS} (population inbreeding coefficient) and population size, as possible variables explaining the differences between populations (Table 1).

Because there were only six populations, the recorded habitat and population characteristics are only used to discuss their possible effects on the differences in performance between populations but no tests were performed.

Results

Comparison of Life-History Traits

The probabilities of mortality, flowering, retrogression, growth and seed production were found to be significantly different between populations within regions (Table 2; Tables S3, S4 in ESM). The probability of mortality was higher for the Slovak Karst populations than the Czech Karst populations (except for population C1, where the

Table 2 Effect of year, stage in the previous year, region, population nested within region and their interactions on mortality, probability of flowering (Prob. of flow.), retrogression and growth

	d.f.	Mortality		Prob. of flow.		Retrogression		Growth	
		Expl. dev.	***	Expl. dev.	***	Expl. dev.	***	Expl. dev.	***
Year	2	0.023	***	0.008	***	0.020	***	0.025	***
Stage in previous year	2	0.291	***	0.150	***	0.268	***	0.229	***
Region	1	0.014	***	0.020	***	0.003	°	0.000	
Population	4	0.015	***	0.020	***	0.024	***	0.010	***
Year×stage in previous year	4	0.014	***	0.009	***	0.000		0.004	
Year×region	2	0.007	**	0.035	***	0.004		0.003	
Region×stage in previous year	2	0.003		0.004	***	0.000		0.000	
Population×year	8	0.009	°	0.034	***	0.007		0.008	
Population×stage in previous year	8	0.008		0.007	**	0.000		0.005	
Year×stage in previous year×region	4	0.008	*	0.002		0.000		0.007	***
Year×stage in previous year×population	16	0.012		0.002		0.000		0.009	

N=2 457 for all analyses; d.f. – degrees of freedom, Expl. dev. – explained deviance. ° – $P < 0.1$, * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$.

probability of mortality was similar to the Slovak Karst populations). In the C2 and C4 populations, probability of mortality significantly differed between years (Table 2, Fig. 4a; Tables S3, S4 in ESM). Although probabilities of flowering were

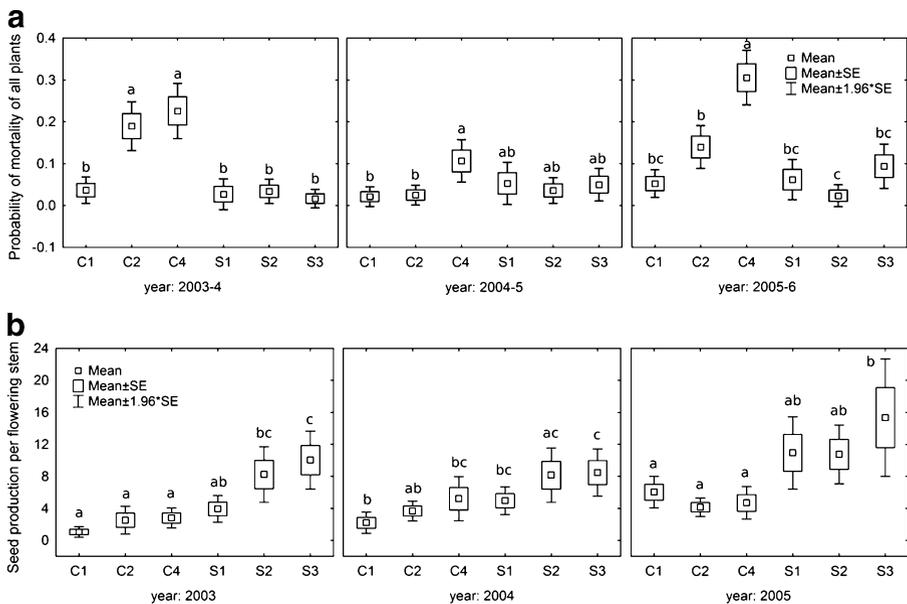


Fig. 4 Probability of mortality of all plants **a** and seed production **b** of *Dracocephalum austriacum* plants and its distribution in six populations and over three transition intervals of the study. The letters in the graph indicate statistically significant differences ($P < 0.05$) between populations within years. C1, C2, C4, S1, S2, S3 are locality codes, C stands for the Czech Karst and S stands for the Slovak Karst

significantly higher in the Slovak Karst populations, there was considerable variability between years and populations (Table 2; Tables S3, S4 in ESM). Only marginally significant differences in the probabilities of retrogression were found between Karst regions (Table 2). However, significant between-population differences were uncovered, and higher retrogression probabilities identified in C2 during the 2003–2004 transition and in C4 during the 2005–2006 transition (Tables S3, S4 in ESM). In addition, there were no significant differences in the probabilities of growth between the Karst regions, but there were significant differences in growth probabilities between populations within regions and between years. In the first year, 2003–2004, higher growth probabilities were identified in comparison with years 2004–2005 and 2005–2006 in all populations (with the exception of S2) (Table 2; Tables S3, S4 in ESM).

Statistically significant higher seed production was also found in the Slovak Karst populations in comparison with the Czech Karst ones ($F_{1,364}=62.35$, $P<0.001$). There were also significant differences in seed production between years and populations, and significant interactions between year and both region and population (Fig. 4b; Table S5 in ESM).

Plant mortality rates decreased with plant size. Seedlings on average were found to have 5.0-fold higher mortality rates than small adult plants and 8.9-fold higher mortality rates than large adult ones in the Czech Karst populations. In the Slovak Karst populations, the mortality rate was 13.2-fold higher for small adult plants and 84.9-fold higher for large adult ones (Tables S1, S2 in ESM). Large adult plants produced on average 5.7-fold more seeds than small adult plants in the Czech Karst and 3.3-fold more seeds in the Slovak Karst population. Germination rates in the field ranged from 0 % to 11.4 % in individual years and populations (Tables S1, S2 in ESM).

Population Performance

Single projection matrices had λ -values (population growth rates) from 0.936 to 1.103 (Table S6 in ESM). All population growth rates were not significantly different from 1 (95 % confidence intervals of λ included 1). The exception was the transition period 2005–2006, when population C4 was significantly decreasing, and the transition period 2003–2004, when population S3 was significantly increasing. Similar results were observed using stochastic population growth rate (λ_S) when data from 2003–2006 were combined. In this case, the population growth rate ranged from 1.017 to 1.152. All studied populations were significantly slightly growing (except for population C4 in the Czech Karst, which was stable (95 % confidence intervals of λ_S included 1)). Results were also similar when all matrices within each region were combined. The stochastic population growth rate (λ_S) was higher in the Slovak Karst region for all years and λ_S was significantly higher in the Slovak Karst populations than in the Czech Karst populations ($P=0.01$; Fig. 5).

In all populations, the highest elasticity was detected for stasis matrix elements (Fig. S1 in ESM). Summed elasticity values for all matrix elements related to stasis ranged from 0.69 to 0.81 between populations. When all matrices from each region were combined, stasis in small and large adult plant stages were the most important transitions in both regions (Fig. S2 in ESM). This indicates that these two regions are very similar in terms of elasticity values.

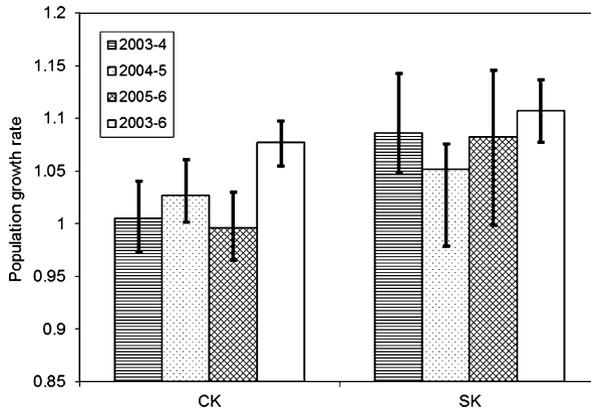


Fig. 5 Stochastic population growth rate (λ_s) and its 95 % confidence interval for all populations from the Czech (CK) and Slovak Karst (SK) combined for each transition interval computed with stochastic simulation models. The last column (white) shows results for all transition intervals combined

According to LTRE analyses, seed and seedling production by large adult plants, germination of seeds, stasis of small adult plants and growth of small to large adult plants are the transitions most contributing to variation in population growth rate in both studied regions. However, we found much higher contributions of seedling growth to small adults and stasis of large adult plants to variation in population growth rate in the Slovak Karst in comparison with the Czech Karst (Fig. 6). Comparing populations over the three transition intervals within the Czech and Slovak Karst regions, no populations were significantly different with respect to their contribution to the overall population growth rate of the given region ($P > 0.18$ in the Czech and $P > 0.45$ in the Slovak Karst region). This indicates that the performance of populations within regions is very similar. There was also no significant variation between single years within regions ($P > 0.60$ in the Czech and $P > 0.08$ in the Slovak Karst region).

Discussion

Our study aimed to describe the spatial and temporal variability in the population dynamics of a critically endangered perennial herb, *Dracocephalum austriacum*, in two distant regions (the Czech and Slovak Karst) with similar habitat conditions, and to evaluate if conclusions concerning factors affecting population performance are comparable between regions. Our results show that populations in the Slovak Karst have a higher long-term population growth rate and are over all performing better than populations in the Czech Karst. The transitions contributing most to the population growth rates are comparable between the two regions with some exceptions. These exceptions, mainly much higher variation between populations and years in seedling growth to small adults and stasis of large adult plants in the Slovak Karst, have to be considered to use the information about population dynamics in one region to understand population dynamics in another region.

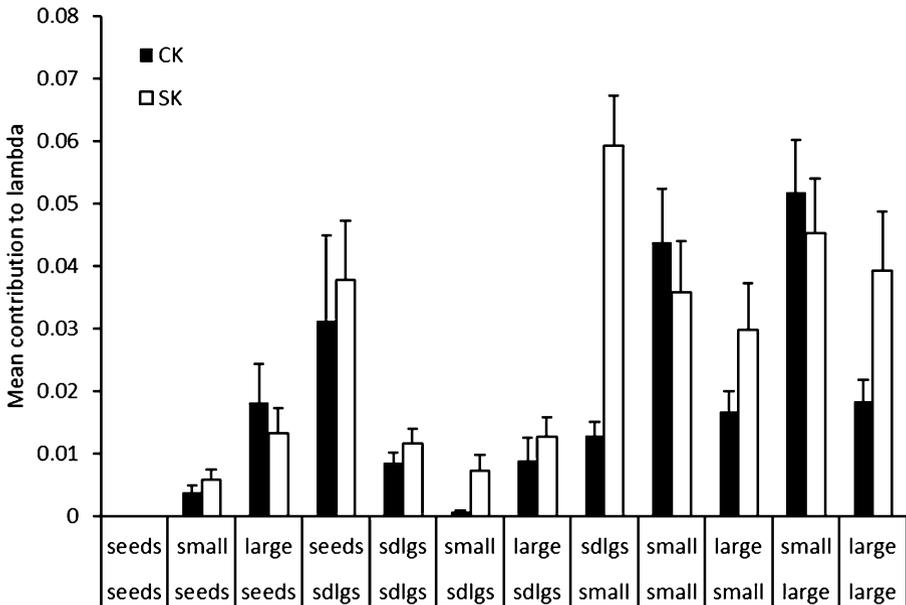


Fig. 6 Comparison of mean contributions of single matrix elements to variation in population growth rate (λ) between the Czech (CK; black bars) and Slovak (SK; white bars) Karst regions based on LTRE analysis. Mean contributions are based on averages of nine matrices within each region (three populations with three transition intervals). Whiskers are standard errors of the means. Labels at the bottom indicate transition from stage in year one (upper label) to stage in year two (lower label). seeds – seeds, sdlds – seedlings, small – small adult plants, large – large adult plants. The transition seed-seed was estimated only in one population in one transition interval and the information on its variation is thus not available

Population Performance

Comparisons of life-history traits between studied regions revealed that populations from the Slovak Karst have higher seed production, lower mortality and increased flowering, although there was significant variability among years and populations. The overall lower mortality and higher seed production in the Slovak Karst populations could result from more suitable habitat conditions in this region. Differences in life-history traits and life-cycle transitions also influenced total population dynamics. The population growth rate computed using stochastic models from 2003–2006 was significantly higher in the Slovak Karst region. Differences between the Czech and Slovak Karst populations are thus evident both from analyses of single life-cycle transitions and overall population dynamics (similarly see Burns et al. 2010; but see Ehrlén 2003; Münzbergová 2005, 2006, 2007; Kolb et al. 2010 for a contrasting pattern).

Although some differences were found in terms of life-history traits and overall population dynamics between the studied regions, they are relatively weak compared to other published studies (e.g., Oostermeijer et al. 1996; Ehrlén et al. 2005). Many authors have demonstrated strong differences in the performance of populations that are very close to each other spatially, but occur in very different habitat conditions. *D. austriacum* is a species with very specific habitat requirements, and thus has been found to occur in very similar habitat conditions throughout its range.

In both regions, seed and seedling production of large adult plants, seed germination, stasis and growth of small adult plants were the transitions that contributed most to variability in population growth rates. In agreement with these results, Fréville et al. (2004) also found that variations in seed production and seedling establishment explained most of the observed variations in population growth rates. They suggested that this variation may be due to differences in the activity of pollinators, the frequency of compatible mates, or the abortion rate due to drift load, which is higher in smaller populations (cf. Colas et al. 2001).

Transitions found to contribute most to the population growth rate are transitions of stasis in small and large adult plant stages and these were also similar in both regions. The low differences between the two regions indicated by elasticity analyses are in agreement with the expectation that transitions with strong effects on population growth rate tend to be conservative (e.g., Ehrlén et al. 2005). Our results are also in agreement with another study on *D. austriacum* performed in France (Andrello et al. 2012). In seven populations of *D. austriacum*, they found that elasticity values associated with stasis of adult plants were always much higher in comparison with those associated with flowering and fecundity.

In our study, we also identified high survival of *D. austriacum* in the seed bank. These seed banks could rescue the population from extinction if the climate and habitat conditions are suitable for germination. An extensive seed bank can be especially important for small populations of *D. austriacum*, which are endangered due to low genetic diversity. The importance of seed banks for the reestablishment of plant populations was shown, for example, by Alexander and Schrag (2003) and Bucharová et al. (2012). Other studies, however, suggest that seed banks alone are not sufficient to reestablish a species that has disappeared from some locality (e.g., Thompson et al. 1997; Baskin and Baskin 1998; Handlová and Münzbergová 2006).

Habitat Conditions

The Czech Karst populations are in localities that are steeper, rockier and with shallower soils in comparison with the populations in the Slovak Karst. The Czech populations are thus more likely to suffer from drought, which could result in higher mortality. Nicolè et al. (2011) also found lower survival and stochastic population growth rate in populations growing on steeper slopes in their study on *D. austriacum* in France. This negative effect of steep slopes was especially apparent in combination with high summer temperatures in the previous year in their study. Similarly, important effects of habitat conditions on various parts of the life cycle were also identified in other studies comparing populations of selected species among regions (e.g., Willems and Ellers 1996; Eckstein et al. 2009).

Genetic Diversity

Lower seed production, overall fitness and population growth rate of the species in the Czech Karst region could also be due to lower genetic diversity and resulting inbreeding depression in this region (Dostálek et al. 2010; Castro et al., unpubl. data). In support of this, a significant positive effect of genetic diversity on plant fitness was also found in a review by Reed and Frankham (2003). Moreover Nicolè (2005) also

found a positive relationship between population viability and heterozygosity in *D. austriacum*. However, it was not confirmed in their subsequent study (Nicolè et al. 2011). They suggest that the correlation between heterozygosity and population viability may have been caused by environmental covariation.

Model Limitations

The high variation in transitions related to reproduction identified using LTRE analysis in our study may be related to the small number of seedlings studied. However, in most cases we studied every seedling we were able to find at each locality, and thus the whole population was studied, not just a sample. Because of this, we have the best possible information on seedling stasis for the given years, and differences in these transitions thus provide information on real differences between populations and transition periods in generative reproduction.

Another possible limitation in our data is the estimation of seed bank survival. Seed bank stasis was estimated using a two-year experiment and we thus do not have information on between-year variability and long-term seed-bank stasis. However, our previous experiment including estimation of seed-bank stasis from the number of viable seeds in the soil confirmed very long seed stasis (Dostálek 2009). Furthermore, when population growth rates with decreased probabilities of seed stasis were calculated, only a very small effect on population growth rate and elasticity was found.

Population viability analyses models must be used with caution, and it has to be kept in mind that they are only models (Beissinger and Westphal 1998; Marrero-Gómez et al. 2007). Accordingly, one must be aware of the limitations of these models, especially when the results are to be used for practical species conservation and management decisions. In the case of the models presented here, it is necessary to point out that it would be better to have studied the populations for a longer period of time, and to have included more regions in our study, so that we could make our results more exact and convincing. Moreover, it would be very useful to test the effects of management policies, such as removal of shrubs, on population dynamics. Thus, further studies should be performed on this system.

Conservation Implications

In the studied populations in the Czech and Slovak Karst regions, the stochastic long-term population growth rates were never significantly below 1 suggesting that the populations are stable and are not currently decreasing. Nevertheless, differences between single populations that could be attributed to various factors, such as the genetic parameters of the populations, soil properties at the localities and weather conditions were found. Although the transitions contributing most to the population growth rates are very similar between the regions there are some exceptions that need to be considered before using information about the most important life-cycle transitions in other regions. We suggest that this conclusion also holds true for other species with narrow habitat requirements occupying very similar habitats, even in very distant regions.

Changes in stasis in small and large adult plant stages had the highest theoretical effect on changes in the population growth rate. These transitions are, however, stable

between populations and years, suggesting that they are not very sensitive to the ongoing changes. Transitions that contribute most to variations in population growth rate should thus be a target of management actions. In both regions these include seed and seedling production by large adult plants, seed germination and stasis and growth of small adult plants. These transitions seem to be affected by climate fluctuations, especially severe droughts and shrub expansion. Reduced genetic diversity and consequential inbreeding also seem to be important factors associated with this variation (Nicolè 2005; Dostálek et al. 2010; but see Nicolè et al. 2011). Although population dynamics was very similar in both regions, there was much higher variability in seedling growth to small adults and stasis of large adults in the Slovak Karst region in comparison with the Czech Karst area. This difference was probably caused by patches of more suitable habitats (deeper soil and less rocky spots) in the Slovak Karst region.

Optimal management actions should thus include protection of small and large adult plants as was also suggested in a recently published study on population dynamics of *D. austriacum* in France (Andrello et al. 2012). This could be done by expanding shrub removal on the localities and public education to prevent illegal collections (Karasová in verb.; Danton and Baffray 1995). Another means of conservation could be to support gene flow between populations. The latter step, however, has to be preceded by explorations of the possible negative consequences of outbreeding depression.

Acknowledgements The authors thank E. Karasová from the Slovak Karst National park for information about the species and help in the field. Workers from the Czech Karst Protected Area Landscape Administration also provided us with information about localities in the Czech Karst region. People from POPEKOL seminars and two anonymous reviewers provided us with many useful comments. This study was supported by GAUK 198/2005, GAČR 526/08/0706, MŠMT 2B06178 and also by a long-term research development project nr. RVO 67985939.

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Received: 24 October 2011 / Revised: 16 March 2012 / Accepted: 29 March 2012 /

Published online: 24 July 2012